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The boundary between the dolphin and its environment is sculpted by blubber - a complex, structural biomaterial. I have investigated the functional design of blubber by (1) measuring its 3-D architecture and its physical connections to other locomotor tissues, and (2) testing its dynamic biaxial stress/strain behavior. Blubber can be biomechanically modeled as an adipose hydrostat: thorax blubber is designed to maximize body volume and tailstock blubber is designed to resist torsion and to store strain energy during swimming. Blubber is directly connected to the axial skeleton in the caudal tailstock, permitting force transmission and limiting shear deformation. Dynamic and pseudostatic mechanical tests have demonstrated that blubber is both a resilient tensile and compressive spring with an elastic modulus similar to that of high-quality biological and synthetic rubbers. Preliminary data demonstrate that blubber resists stress-relaxation. Blubber is morphologically and mechanically well-suited to (1) limit large scale shear deformation that might occur across the skin's thickness and (2) function as a biological spring. This study is the first to present data that support the hypothesis that blubber may function as a spring to decrease the metabolic cost of swimming in dolphins.

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PRINCIPLE INVESTIGATOR: D. A. Pabst

INSTITUTION: University Of North Carolina at Wilmington

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OBJECTIVE: The boundary between the dolphin and its aquatic environment is sculpted by blubber - a complex, structural biomaterial. I have investigated the functional design of blubber by (1) measuring its regionally specific 3-D architecture and its physical connections to other locomotor tissues, and (2) testing its dynamic biaxial and uniaxial stress/strain behavior. I have used these data to create morphologically accurate computer images of blubber microstructure and to create mechanically accurate physical models of this biomaterial. This study has yielded information needed to evaluate blubber's mechanical roles during swimming and a model useful to future biomimetics studies of hydrodynamically tuned, pliant composite biomaterials.

APPROACH: I used blubber from fresh and fresh frozen cetaceans that had stranded or been taken incidental to fishing operations. Frozen blubber samples were serially sectioned in three orthogonal planes: transverse, longitudinal and tangential. Sections are viewed through polarized light to visualize birefringent collagen fibers. The microscopic images of blubber sections were used to measure (1) collagen fiber size (diameter and length within the plane), (2) collagen fiber angle relative to major body planes, and (3) cross-sectional area of section occupied by fibers and cells (i.e. density of constructional element) using computerized image analysis software. Serial sections were used to reconstruct the 3-D fiber morphology of blubber using computer aided design (DesignCad 3D). I performed mechanical tensile tests on blubber in the lab of Dr. John Gosline, in the Zoology Department at the University of British Columbia. I traveled to the BioDesign Studio, at Duke University to build biomimetic blubber models of increasing morphological complexity.

ACCOMPLISHMENTS: (1) Our lab created an archival collection of fresh, frozen blubber, dorsal fin and fluke samples from over fifty common (*Delphinus delphis*), and bottlenose (*Tursiops truncatus*) dolphins, and harbor porpoise (*Phocoena phocoena*). These tissues were collected from animals that had undergone a systematic necropsy protocol. Thus, quantitative analyses of collagen fiber architecture of blubber could be integrated with data series on whole body tissue compartments in delphinid and phocoenid cetaceans.
(2) We completed quantitative morphological analyses of lateral flanking blubber in the bottlenose dolphin at longitudinal positions in the thorax and caudal tailstock. Comparisons of serial sections through blubber in orthogonal, tangential and longitudinal planes have demonstrated statistically significant differences in collagen fiber architecture (a) across planes (b) throughout its depth and (c) between homologous positions at both locations. Blubber is reinforced with two sets of fibers: radial fibers that traverse the thickness of blubber and circumferential fibers that wrap around the dolphin. Radial fibers in

the hypodermis of the thorax and tailstock are oriented at 45° to both transverse and longitudinal planes. Cranial and caudal leaning circumferential fibers in thorax blubber wrap the animal at approximately 55°. In tailstock blubber, cranial fibers wrap at approximately 45° and caudal fibers at approximately 70°.

(3) Based upon fiber angle measurements, we have generated a biomechanical model of blubber. Blubber is an adipose hydrostat, reinforced with collagen at appropriate angles to experience tensile strains both during extension and compression. Thorax blubber is reinforced at angles that maximize the volume of the dolphin cylinder. Tailstock blubber is reinforced to resist torsional forces and to store elastic strain energy.

(4) We have demonstrated that in the region of the caudal tailstock, blubber is directly attached to the axial skeleton.

(5) We have demonstrated that the collagen fiber architecture of the keel is dramatically different than lateral flanking blubber. The caudal region of the dorsal keel appears to be reinforced laterally with longitudinally oriented fibers. This collagen fiber morphology is shared with the flukes and dorsal fin.

(6) We have demonstrated that blubber is a resilient, non-linearly elastic, highly-ordered biocomposite. Dynamic and pseudostatic mechanical tests of blubber have demonstrated that it is both a resilient tensile (68-97% energy recovery) and compressive (53-86% energy recovery) spring with an elastic modulus similar to that of high-quality biological and synthetic rubbers (1-3 MPa). Preliminary data also demonstrate that blubber resists stress-relaxation.

(7) Uniaxial tensile tests of whole caudal keel structures from bottlenose dolphin and harbor porpoise demonstrated that blubber's mechanical properties vary regionally: blubber becomes three orders of magnitude stiffer as you progress from the region of the dorsal fin to the insertion of the tail flukes. Thus, the mechanical properties of the keel blubber-structure are regionally tuned.

(8) With BioDesign Studio, we have built the first biomimetic models of dolphin blubber. A model, reinforced only with circumferentially oriented fibers assumes a saddle-shape when bent, suggesting emergent shape properties based upon the fiber architecture of the composite.

CONCLUSIONS: (1) Blubber can be biomechanically modeled as an adipose hydrostat: adipose cells function as the compression-resisting member, and circumferentially and radially oriented collagen fibers function as tensile members. (2) Thorax blubber is designed to maximize dolphin cylinder volume and tailstock blubber is designed to resist torsional loading and to store elastic strain energy during tail oscillations. Radial fibers in both regions are oriented to minimize shear deformation across the thickness of the skin. (3) Blubber functions to intimately connect the skin to the underlying axial skeleton in the flexible caudal tailstock, permitting force transmission and limiting shear deformation. (4) Blubber functions as a highly resilient, non-linearly elastic spring with an elastic modulus similar to that of high-quality synthetic rubbers (1-3 MPa). Blubber's mechanical properties, like its morphological constructions, vary regionally. (5) Biomimetic models of blubber reveal emergent shape-generating functions of fiber-reinforcement of thick composites.

SIGNIFICANCE: This study has demonstrated that blubber is morphologically and mechanically well-suited to (1) limit large scale shear deformation that might occur across the skin's thickness and (2) function as a biological spring. Blubber's non-linear stress-strain curve suggests that it can function as a spring in parallel with the dolphin's axial swimming muscles (similar to the parallel springs in swimming invertebrates). Blubber's initial low-modulus behavior requires little muscular force be diverted to loading the blubber spring during the mid-phase of the stroke, when the swimming muscles are performing maximal hydrodynamic work. When the potential for doing useful hydrodynamic work decreases near the end of the stroke, blubber's increasing stiffness permits elastic strain energy storage. This study is the first to demonstrate that blubber, an adipose hydrostat, may function as a biological spring to decrease the metabolic cost of swimming in dolphins.

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